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Laelapine Mite (Acari: Laelapidae) Morphometric Analysis Reflects Taxonomic and Geographic Clusters of South American Oryzomyines (Rodentia: Sigmodontinae)

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Abstract

Ongoing efforts to survey and inventory nonvolant small mammals across the Neotropics are beginning to reveal a highly structured and diverse fauna of rodents and marsupials. By increasing the foundation of specimens in museums around the world, it has become possible, for the first time, to evaluate and quantify the similarities and differences among small mammals collected from a broad range of geographic localities, ecoregions, and habitats. Because ectoparasites were sampled in the process of collecting mammalian voucher specimens, we are able to study the laelapine mites (Acari: Laelapidae) associated with well-identified and verifiable host specimens. Here, we evaluate morphometric variation of two nominal mite species, *Laelaps acuminata* and *Gigantolaelaps oudemansi* (Acari: Laelapidae), that are widespread and appear to infest a wide range of both terrestrial (*Hylaeamys* and *Euryoryzomys*) and arboreal (*Oecomys*) oryzomyine rodents. Mites were collected from seven species (three genera) of oryzomyines, *E. macconnelli*, *E. nitidus*, *E. russatus*, *H. megacephalus*, *Oe. bicolor*, *Oe. concolor*, and *Oe. mamorae*, from a number of localities from Bolivia, Brazil, and Paraguay. Results of both UPGMA clustering and principal component analyses, for both mite species, indicate that each rodent species hosts distinct mite species (with one possible exception—*Euryoryzomys nitidus* and *E. russatus*), and that each of these two nominal mite species is actually a complex of species, heretofore unrecognized, and awaiting formal description. Our results add to the growing body of evidence that laelapine mite species are host-specific, rather than pleioxenous, as has been the paradigm developed in the parasitological literature. Finally, we discuss the implications of our results for oryzomyine taxonomy, including the status of *Euryoryzomys nitidus* and *E. russatus*. These morphometric studies indicate that the diversity of the laelapine mite fauna associated with oryzomyine rodents has been underestimated.

Resumo

Levantamentos e inventários de pequenos mamíferos não voadores em toda a Região Neotropical estão começando a revelar uma fauna de roedores e marsupiais bem estruturada e altamente diversa. Ao aumentar a base de espécimes em museus de todo o mundo, tornou-se possível, pela primeira vez, avaliar e quantificar as semelhanças e diferenças entre pequenos mamíferos coletados a partir de uma ampla gama de localizações geográficas, ecorregiões e ambientes. Devido aos ectoparasitas terem sido amostrados no processo de coleta de espécimes-testemunho de mamíferos, somos capazes de estudar os ácaros laelapíneos (Acari: Laelapidae) associados às amostras de hospedeiros precisamente verificados e identificados. Neste estudo, avaliamos a variação morfométrica de duas espécies nominais de ácaros, *Laelaps acuminata* e *Gigantolaelaps oudemansi* (Acari: Laelapidae), que são comuns e parecem infestar uma grande

quantidade de roedores Oryzomyini, tais como os terrestres pertencentes aos gêneros *Hylaeamys* e *Euryoryzomys*; e o arbóreo pertencente ao gênero *Oecomys*. Nossos espécimes-testemunho de ácaros foram coletados a partir de sete espécies (pertencentes a três gêneros) de roedores Oryzomyini, *E. macconnelli*, *E. nitidus*, *E. russatus*, *H. megacephalus*, *Oe. bicolor*, *Oe. concolor*, and *Oe. mamorae,* provenientes de uma série de localidades do Brasil, do Paraguai e da Bolívia. Os resultados de ambas as análises de agrupamento e de componente principais para ambas as espécies de ácaros, indicam que cada espécie de roedor hospeda espécies distintas de ácaros (com uma possível exceção: *Euryoryzomys nítidus* e *E. russatus*). Além disso, cada uma dessas duas espécies nominais de ácaros representa um complexo de espécies até então desconhecido e aguardando uma descrição formal. Nossos resultados acrescentam ao corpo de evidencia de que espécies de ácaros laelapineos são hospedar específico, ao invés de pleioxenous como a paradigma desenvolvido na literatura parasitológico. Finalmente, discutimos as implicações do nossos resultados, taxonomia de oryzomyineos, incluindo a status de *Euryoryzomys nitidus* e *E. russatus*. Estes estudos morfométricos implicam que a diversidade da fauna de acaros laelapideos associada com roedores oryzomyineos tem sido subestimada.

Resumen

Los estudios e inventarios que se están realizando sobre pequeños mamíferos no voladores por todo el Neotrópico están comenzando a revelar una fauna de roedores y marsupiales con estructura compleja y diversa. Por el creciente establecimiento de buenas colecciones de especímenes en museos alrededor del mundo, ha llegado a ser posible, por primera vez, la evaluación y cuantificación de semejanzas y diferencias entre pequeños mamíferos colectados de un gran rango de localidades geográficas, ecorregiones, y hábitats. En este trabajo, evaluamos variaciones morfológicas de dos especies nominales de ácaros, *Laelaps acuminata* y *Gigantolaelaps oudemansi* (Acari: Laelapidae), de amplia distribución y al parecer infestan en un rango extenso de roedores oryzomyine ambos terrestre (*Hylaeamys* and *Euryoryzomys*) y arborícola (*Oecomys*). Nuestros especímenes de ácaros fueron colectados de siete especies (tres géneros) de roedores oryzomyine, *E. macconnelli*, *E. nitidus*, *E. russatus*, *H. megacephalus*, *Oe. bicolor*, *Oe. concolor*, and *Oe. mamorae,* de varias localidades de Brasil, Paraguay y Bolivia. Varios de los especímenes huéspedes de los cuales nuestros ácaros fueron colectados, fueron los mismos especímenes examinados y reportados en una importante monografía de revisión, permitiéndonos así apoyar y argumentar directamente algunas conclusiones taxonómicas de ese trabajo.

Resultados de ambos agrupamientos UPGMA y análisis de componente principales, de ambas especies de ácaros, indicaron que cada especie de roedor hospeda distintas especies de ácaros (con una posible excepción—*Euryoryzomys nitidus* y *E. russatus*), y que cada una de estas dos especies de ácaros nominales son en realidad un complejo de especies, hasta ahora no reconocido, y esperando una descripción formal. Nuestros resultados suma a la creciente evidencia que las especies de ácaros laelapine son extremadamente huésped-especifico, antes que pleioxenous, como ha sido el paradigma desarrollado en la literatura parasitológica. Finalmente, discutimos las implicancias de nuestros resultados para la taxonomía oryzomyine, incluyendo el estatus de *Euryoryzomys nitidus* y *E. russatus*.

Keywords: ectoparasites, *Euryoryzomys*, *Gigantolaelaps*, host–parasite relationships, *Hylaeamys*, *Laelaps*, Morphometrics, Oryzomyini

Laelapine mites (Mesostigmata: Laelapidae) are the most diverse group of arthropods infesting Neotropical oryzomyine rodents (Rodentia: Cricetidae: Sigmodontinae), and are usually the most abundant ectoparasites sampled by brushing the pelage of these hosts at capture. However, knowledge of the host specificity of these associations has been confounded by a lack of information about the taxonomy of both mammals and arthropods. It is common for specialists working with these ectoparasites to assume that species boundaries of mammals are well-known, and this has led to misunderstandings about the host–mite distributional patterns.

However, it has been clear since Furman's (1972) classic survey paper on Venezuelan laelapines that species in the genus *Gigantolaelaps* are specific to oryzomyine rodents, and species in *Laelaps*, with the exception of a few distinct species, are also primarily associated with this tribe of rodents (Gettinger, 1987, 1992a; Gettinger et al., 2005; Martins-Hatano et al., 2002). An examination of "host association patterns" suggests that in the neotropics, laelapine

mites are taxon-specific, either "stenoxenous" (each species infesting congeneric hosts), or "pleioxenous" (each species of mite infesting hosts of several closely related host genera). These relationships are not easy to explain ecologically, because mammal species that are closely related phylogenetically are not often encountered in the same microhabitats, and close encounters are necessary for transfers of mites between host individuals. However, the concept persists because of the hypothesis that the mites may be more compatible, physiologically or immunologically, with closely related hosts. This may be true for clearly parasitic arthropods, but laelapines are poorly adapted for blood feeding, and are only rarely observed carrying blood in their gut. Instead, laelapines are phoretic in the fur of their oryzomyine hosts, and the populations sampled are strongly biased toward adult females, each carrying either an egg or embryonic offspring. Since most oryzomyine rodents are thought to be solitary and territorial mammals, and laelapine mite infestations are driven by dispersal factors, colonization events should occur primarily between conspecific hosts (probably at copulation and from mother to young prior to weaning).

The taxonomy of laelapine mites associated with Neotropical small mammals has a solid, though conservative foundation. Furman's (1972) taxonomic keys to *Gigantolaelaps* and *Laelaps* of South America are easy to use, and still function well to separate, and tentatively identify these mites in surveys. The species that have been described more recently (see Gettinger, 1992b; Gettinger & Gardner, 2005; Gettinger et al., 2011b) are easily diagnosed and distinguished from the mites included in Furman's key. However, because of growing concern over habitat destruction and threats to biodiversity, a new emphasis has arisen concerning species delimitation, the methods by which species boundaries are determined, and how new species are discovered. Species are the fundamental units of analysis in conservation biology and also in ecology, biogeography, systematics, and evolution. The failure to correctly diagnose species boundaries of both mites and mammals continues to confound efforts to understand their coevolutionary history, as well as to develop coherent conservation strategies.

The Oryzomyini comprise by far the most speciose tribe of neotropical sigmodontine rodents, an ecologically and morphologically diverse taxon with species distributed from the southeastern United States to the southern cone of South America (Prado and Percequillo, 2013). Although an inclusive diagnosis of the tribe was provided by Voss and Carleton (1993), the nomen "*Oryzomys capito*" continued to be used to identify a complex of terrestrial oryzomyines varying in body size and pelage types, and distributed across a wide range of neotropical macrohabitats. Although many mammalogists suspected this was a composite taxon (comprised of species distributed through several genera), it required the gathering of an extensive set of specimens, from many institutions to begin to resolve the problem. A comprehensive taxonomic revision (Musser et al., 1998) of the large complex of terrestrial oryzomyine rodents formerly classified as "*Oryzomys capito*", clearly divided these taxa, using morphological, distributional, and chromosomal evidence. Beginning to solve the complexities of this large group had the effect of opening up the entire tribe Oryzomyini to more comprehensive taxonomic revision. Weksler et al. (2006) and Weksler (2006) corroborated Voss and Carleton's (1992) hypothesis that the Oryzomyini is monophyletic, described new genera, and divided the assemblage into four distinct clades (A,B,C, and D) based on morphological and molecular characters.

This acarological study was originally inspired by the analyses of Musser et al. (1998), with the "*O. capito* complex," and we examine laelapine mites associated with both terrestrial and arboreal oryzomyine rodents (clade B of Weksler, 2006). In particular, we analyze the morphometric relationships of two nominal laelapine species, *Laelaps acuminata* Furman, 1972 and *Gigantolaelaps oudemansi* Fonseca, 1939, infesting the oryzomyine rodent hosts, *Hylaeamys megacephalus* (Fischer,1814), the *Euryoryzomys* "*nitidus* group" [(*E. macconnelli* (Thomas, 1910); *E. nitidus* (Thomas, 1884)and *E. russatus* (Wagner, 1848)], a group of species "formerly known as *O. capito*," as well as three species of *Oecomys* [*Oe. bicolor* (Tomes, 1860), *Oe. concolor* (Wagner, 1845), and *Oe. mamorae* (Thomas, 1906)]. The results of these comparisons support the alignment proposed by Weksler et al. (2006), Weksler (2006), provide insight regarding probable biological species boundaries within the two nominal mite species, and allow us to make an independent assessment of the species boundaries and geographic distributions of their oryzomyine rodent hosts. Because ectoparasites were collected from some of the mammal vouchers that were studied by Musser et al. (1998), we were able to examine mites directly linked with their revisionary research (these vouchers are marked with asterisk in Appendix 1), thus enabling us directly to compare the taxonomic and geographic structure of the mite populations, with the pertinent results of that monograph.

Materials and Methods

Laelapine mites were sampled from 71 individual hosts representing seven species of oryzomyine rodents from Bolivia, Brazil, and Paraguay (Appendix 1). A generalized description of ectoparasite sampling techniques is found in

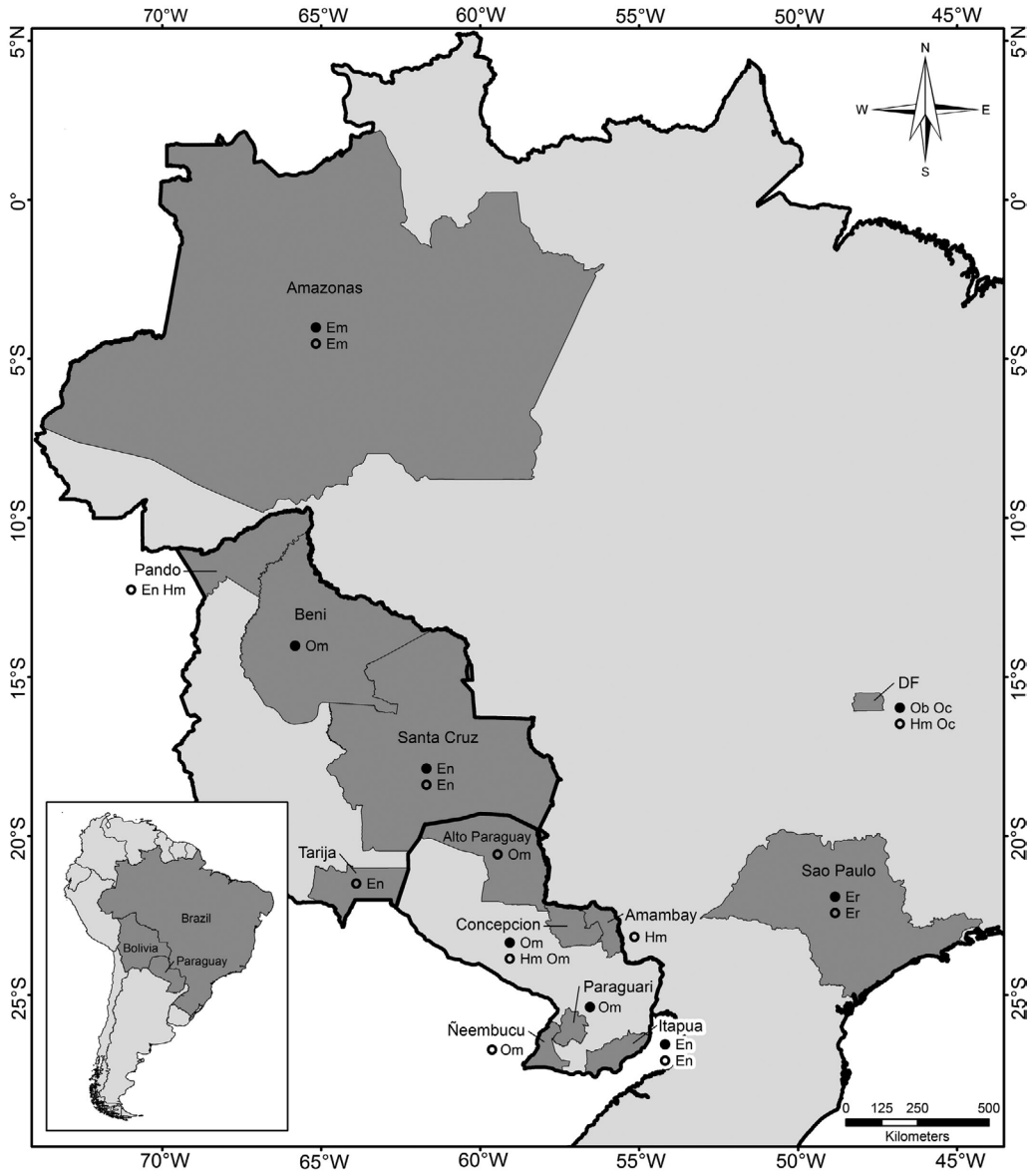

Figure 1. Map of states (Brazil) and departments (Paraguay and Bolivia) from which specimens were analyzed in this study. Shading of states and departments indicates that *Laelaps acuminata* (closed circles) and/or *Gigantolaelaps oudemansi* (open circles) were used from that area. Letter codes indicate host species of mammals from which mites were sampled: Em, *Euryoryzomys macconnelli*; En, *E. nitidus*; Er, *E. russatus*; Hm, *Hylaeamys megacephalus*; Ob, *Oecomys bicolor*; Oc, *Oe. concolor*; Om, *Oe. mamorae*.

Gettinger (1992a); a rigorous sampling protocol was employed in all of these surveys to minimize inter-host contamination of parasites. All mite specimens used in this study were mounted individually in Hoyer's medium, ringed with glyptal, and measured with an ocular-scale calibrated with a stage micrometer. All mite specimens were prepared, identified, and measured by DG. Only adult female mites were analyzed; they represented the most abundant life stage found on host mammals. Furthermore, laelapid mite taxonomy is based primarily on adult females.

From each host individual, one to six specimens were selected for measurement. In total, 54 specimens of *Laelaps acuminata* and 55 of *Gigantolaelaps oudemansi* were analyzed (Appendix 1). The *L. acuminata* were collected from six species of rodents from the states of Amazonas and São Paulo and the Federal District (Brazil); the departments of Concepción, Itapúa, and Paraguarí (Paraguay); and the departments of Beni and Santa Cruz (Bolivia). Specimens of *G. oudemansi* were collected from six species of rodents from the states of Amazonas and São Paulo and the Federal District (Brazil); the departments of Alto Paraguay, Amambay, Concepción, Itapúa, and Ñeembucú (Paraguay); and departments of Pando, Santa Cruz, and Tarija (Bolivia) (Figure 1). The ectoparasite specimens are deposited at the

Harold W. Manter Laboratory, University of Nebraska (Lincoln, USA). The repositories and catalog numbers of host voucher specimens are provided in Appendix 1.

Thirty-seven continuous characters were chosen to represent different regions of the laelapid body, some because they diagnose taxa and others as representative descriptors of size and shape of mites. The precision of the dataset taken from the mites was determined by measuring a single specimen ten times for all characters. Final determination of which characters to use was predicated on a low coefficient of variation in these tests. Many of the characters are bilateral and when variable, we always chose the longer measurement, assuming that this variation is usually due to breakage or orientation of the structure on the slide. Mite specimens were selected at random for measurement, but were included only if all 37 characters could be clearly seen and measured.

General morphological terminology follows Krantz & Walter (2009). The body regions and characters included the following (with shorthand designations of characters provided in parentheses): Dorsal Shield —dorsal shield length (DSL), dorsal shield width at midlevel (DSW); Dorsal Chaetotaxy—distance between j5 setae (j5-j5), distance between z5 setae (z5-z5), length of j5 (j5L), length of z5 (z5L), distance between J5 setae (J5-J5), distance between Z5 setae (Z5-Z5), length of J5 (J5L), length of Z5 (Z5L); Gnathosoma—distance between capitular setae (CAP-CAP), length of capitular setae (CAPL), length of inner hypostomatic setae (INNL), distance between capitular and inner hypostomatic setae (CAP-INN); Sternal Shield—length of sternal shield (SSL), width of sternal shield at level of second sternal setae (SSW), distance between first sternal setae (S1-S1), distance between third sternal setae (S3-S3), length of anterior sternal setae (S1L), length of posterior sternal setae (S3L); Epigynial Shield—length of epigynial shield (ESL), distance between epigynial setae (E5-E5), greatest width of epigynial shield (ESW), length of poststernal setae (S4L), length of epigynial setae (E5L); Anal Shield—length of paranal setae (PARAL), length of postanal seta (POSTL), distance from postanal seta to anterior midline of anal shield (POST-EDGE), distance between paranal setae (PARA-PARA), greatest width of anal shield (ASW); Legs—length of proximal seta coxa I (PROXCOX), length of distal seta coxa I (DISTCOX), length of posterior seta coxa II (POSTCOX2), length of posterior seta coxa III (POSTCOX3), length of posterior seta coxa IV (POSTCOX4), length of anterior dorsal seta femur I (DFEM1L), length of posterior dorsal seta genu I (DGEN1L).

Morphometric relationships were evaluated separately for *L. acuminata* and *G. oudemansi*. For these analyses, each of the 37 linear measurement characters was standardized to a mean of zero and a standard deviation of one in order to mitigate the influence of size variation among characters on the phenetic relationships among individuals.

To evaluate relative variation among: (1) mites from the same host individual, (2) mites from different individuals of the same host species from the same locality, (3) mites from the same host species from geographically diverse localities, and (4) mites from different host species, a matrix of average taxonomic distances among specimens was calculated from the matrix of standardized characters for each of the two mite species. The average taxonomic distance is equivalent to the Euclidean distance in character space, where no characters are missing, which was the case with our data set (Rohlf, 2009). A phenogram was then constructed from this distance matrix, utilizing the Unweighted Pair-Group Method using Arithmetic Averages (UPGMA). The cophenetic correlation coefficient (Rohlf, 2009) was calculated as an indicator of how well the phenogram represents the original standardized data.

Principal Component Analysis (PCA) was used to evaluate morphometric variation among the mites of each species, and to define and visualize clusters within the nominal mite species, as well as to evaluate the contributions of individual characters to the phenetic differences among clusters (Sneath & Sokal, 1973). Eigenvectors were extracted from a pair-wise matrix of Pearson product-moment correlations of the standardized characters. The original matrix of standardized measurements was then projected onto the eigenvectors, and a two-dimensional plot was constructed based on the characters' projections onto principal components 1 and 2. These graphs enable visualization of inter-individual relationships in the two-dimensional space that best represents the complete (37-dimensional) character space. In addition, a minimum spanning tree among the 54 (for *L. acuminata*) or 55 (*G. oudemansi*) individuals was calculated from inter-individual distances based on the standardized characters, and this tree was mapped onto the two-dimensional plot. This enhanced visualization of relative inter-individual distances and enabled detection of distortions in the relationships as depicted in the two-dimensional models.

Although the PCA of all specimens (for both mite species) showed clear separation among most host taxa, additional PCAs of mites from congeneric host species were employed to further detect and visualize separation of clusters based on host species and geographic origin, and to elucidate patterns of morphometric variation characteristic of mites infesting that particular host genus. Moreover, for both *L. acuminata* and *G. oudemnsi*, specimens infesting *Euryoryzomys nitidus* and *E. russatus* clustered closely together; thus an additional PCA was performed in order to assess more precisely the morphometric variation among populations of mites infesting these two host species.

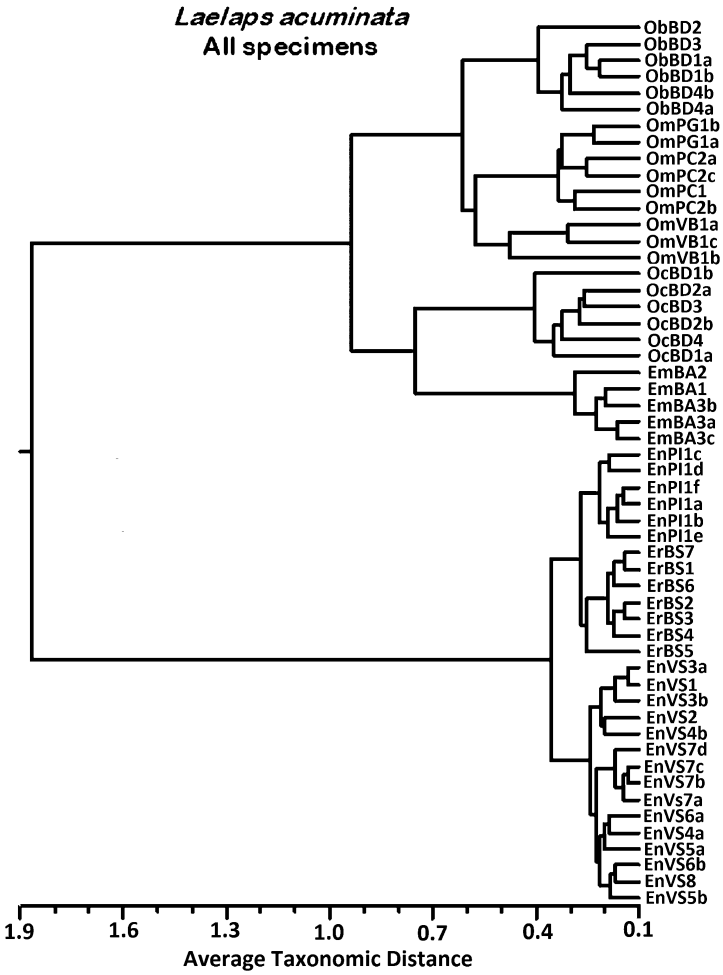

Figure 2. Phenogram depicting morphometric relationships among all *Laelaps acuminata* examined in this study. OTU codes refer to host species, locality, and individual: 1st and 2nd (letters), genus and species (Em, *Euryoryzomys macconnelli*; En, *E. nitidus*; Er, *E. russatus*; Ob, *Oecomys bicolor*; Oc, *Oe. concolor*; Om, *Oe. mamorae*); 3rd (letter), country (B, Brazil; P, Paraguay, V, Bolivia); 4th (letter), state (or department) (BA, Amazonas; BD, Distrito Federal; BS, São Paulo; PC, Concepción; PG, Paraguarí; PI, Itapúa; VB, Beni; VS, Santa Cruz); 5th (number), host individual sequence number, of that species and state; 6th (lower-case letter, where present), mite individual sequence number of that species, state, and host individual. The cophenetic correlation coefficient is 0.942.

Results

Laelaps acuminata

All specimens.—The phenogram of all *L. acuminata* examined (Figure 2) shows two primary clusters of specimens, one of those mites from *Euryoryzomys nitidus* and *E. russatus*, and the other of the remaining host species. Three secondary clusters are found within the first primary cluster—(1) *E. nitidus* from Paraguay, (2) *E. russatus* (from Brazil), and (3) *E. nitidus* from Bolivia. The Paraguayan *E. nitidus* and the Brazilian *E. russatus* form a cluster to the exclusion of the Bolivian *E. nitidus*.

The other large cluster included the mites from three species of *Oecomys* plus those from *E. macconnelli*. Within this larger cluster, the mites from each of the four host species cluster separately from mites infesting other host species. One host species is represented by two localities; the mites from Paraguayan *Oe. mamorae* cluster separately from those from Bolivia.

A combination of the first two principal components (PC-1 and PC-2) clearly separates specimens of *L. acuminata* from each host taxon from those from all other host taxa, with the exception of *Euryoryzomys nitidus* and *E. russatus* (Figure 3). PC-1 accounts for 89.7% of the variance in this data set, and all 37 characters load strongly and positively on this component (Table 1). This is therefore a generalized size component, with the smallest mites

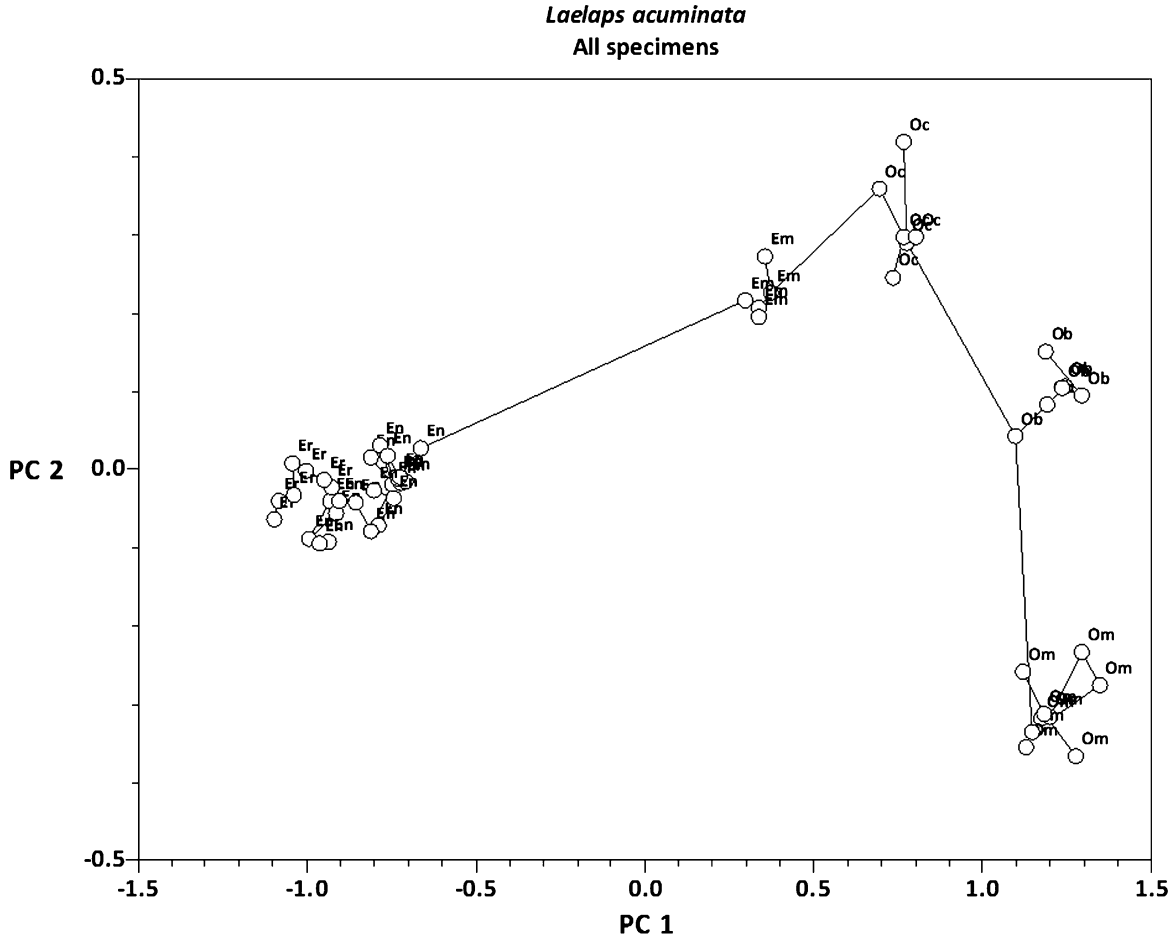

Figure 3. Matrix plot (PC 1 × PC 2) of all *Laelaps acuminata* examined in this study. OTU codes indicate genus and species of host animal: Em, *Euryoryzomys macconnelli*; En, *E. nitidus*; Er, *E. russatus*; Ob, *Oecomys bicolor*; Oc, *Oe. concolor*; Om, *Oe. mamorae*. See Table 1 for character loadings on PC 1 and PC 2, and eigenvalues of these two components.

(from *E. nitidus* and *E. russatus*) about two standard deviations smaller than the largest (from *Oecomys bicolor* and *Oe. mamorae*), on average, and the mites from *E. macconnelli* and *Oe. concolor* intermediate in size. PC-2, with an eigenvalue of 1.3 (3.5% of the variance), is the only other "important" component in this data set (i.e., eigenvalue >1.0, which would be the eigenvalue of a character that was uncorrelated with any other characters), and although no characters load strongly on it, mites of the three *Oecomys* species are clearly separated from each other by PC-2. All dorsal shield and anal shield characters load positively on this component, and all but one of the leg seta characters load negatively. Thus it appears that the *L. acuminata* of *Oe. concolor* (along with those of *E. macconnelli*) have larger dorsal and anal shield characters, and longer anal shield setae and shorter leg setae, than do the mites of *Oe. mamorae* (at the other extreme of PC-2) or *Oe. bicolor* (intermediate on PC-2).

***Euryoryzomys* spp.**—*L. acuminata* from these three host species can be separated by a combination of the first two principal components of variance (Figure 4). PC-1 represents 83.5% of the variance, has 34 of 37 characters strongly and positively associated with it (Table 1), and thus is a general size component. PC-1 separates mite from *E. macconnelli* from those from *E. nitidus* and *E. russatus*, with the *E. macconnelli* mites being two to three standard deviations larger than the others. PC-2 accounts for 5.9% of the variance among these mites, and has two leg setal characters strongly and negatively associated with it. On this axis, mites from Brazilian *E. russatus*, Paraguayan *E. nitidus*, and Bolivian *E. nitidus* form an apparently continuous gradient, with the *E. russatus* mites being most positive (i.e., with lower values for the two leg characters), with Bolivian *E. nitidus* at the negative extreme, and those from Paraguayan *E. nitidus* intemediate along this axis.

Table 1. Eigenvectors (character loadings) and eigenvalues for PC 1 and PC 2, for all principal components analyses reported in this study. Characters with loadings ≥ 0.700 are considered to be strong loadings (whether positive or negative) on PC 1 (or ≥ 0.600 for PC 2), and are printed in bold face to facilitate viewing. Eigenvalues for each component are listed at the bottom of the table, along with the percentage of the variance represented by each eigenvalue. An eigenvalue ≥ 1.0 is considered to be "important" (incorporating more of the overall variance than a single character represents). Although most of the analyses resulted in > 2 components with eigenvalues > 1.0, a combination of the first two components was sufficient to distinguish among clusters (mites from distinct host species and/or localities), in all analyses.

	Laelaps acuminata								*Gigantolaelaps oudemansi*									
Body regions	All host taxa		*Euryoryzomys*		*E. nitidus* & *russatus*		*Oecomys*		All host taxa		*Euryoryzomys*		*E. nitidus* & *russatus*		*Oecomys*		*H. megacephalus*	
and characters	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2
Dorsal shield																		
DSL	**0.985**	0.123	**0.987**	0.100	**0.801**	0.165	0.380	**0.860**	**0.970**	0.032	**0.841**	0.369	0.473	0.545	**0.914**	0.253	**0.911**	0.285
DSW	**0.959**	0.245	**0.976**	-0.067	**0.852**	0.113	-0.515	**0.742**	**0.933**	0.179	**0.900**	-0.327	**-0.866**	0.194	**-0.747**	-0.281	**0.927**	0.172
Dorsal chaetotaxy																		
j5–j5	**0.936**	0.054	**0.916**	0.045	0.532	-0.187	0.405	0.394	0.562	0.243	**0.831**	0.166	-0.124	-0.395	**-0.917**	-0.272	**0.815**	-0.150
z5–z5	**0.960**	0.176	**0.918**	0.238	0.118	**0.793**	-0.294	0.324	**0.923**	0.159	**0.831**	0.345	0.217	-0.349	0.515	-0.031	**0.805**	-0.264
j5L	**0.895**	-0.412	**0.945**	0.296	-0.295	**0.620**	**0.987**	0.025	**0.720**	**0.612**	**0.870**	-0.160	-0.635	-0.041	-0.476	0.063	0.696	-0.352
z5L	**0.908**	-0.375	**0.953**	0.280	-0.260	**0.602**	**0.973**	0.092	**0.743**	0.565	**0.716**	0.192	0.014	0.421	-0.427	-0.106	**0.745**	-0.508
J5–J5	**0.971**	0.023	**0.939**	0.021	0.622	0.052	0.367	-0.286	0.072	-0.510	0.447	-0.539	**-0.749**	-0.135	0.147	-0.084	0.553	-0.481
Z5–Z5	**0.918**	0.111	**0.914**	-0.167	**0.767**	0.095	-0.119	-0.361	0.487	**0.693**	0.390	-0.507	-0.603	0.109	**-0.872**	-0.276	0.572	-0.472
J5L	**0.962**	-0.169	**0.897**	0.383	-0.528	0.368	**0.900**	0.057	**0.827**	0.252	0.183	**-0.847**	**-0.876**	-0.007	-0.621	-0.417	0.663	0.093
Z5L	**0.988**	-0.011	**0.967**	-0.150	**0.897**	0.000	0.693	0.041	**0.885**	-0.329	0.673	-0.390	-0.558	**0.668**	0.647	-0.065	**0.828**	-0.131
Gnathosoma																		
CAP–CAP	**0.972**	-0.004	**0.949**	0.155	0.259	-0.338	**0.757**	-0.102	0.624	0.072	0.653	-0.406	**-0.708**	-0.242	0.488	**-0.655**	**0.713**	0.028
CAPL	**0.892**	0.020	**0.974**	-0.009	**0.761**	0.120	**0.722**	0.187	**0.711**	-0.572	0.576	-0.530	**-0.799**	-0.027	**-0.868**	0.213	**0.724**	0.203
INNL	**0.952**	-0.089	**0.974**	-0.028	**0.769**	-0.241	**0.838**	0.207	**0.839**	-0.427	0.684	0.344	0.228	-0.013	**-0.976**	-0.046	**0.834**	0.054
CAP–INN	**0.983**	-0.003	**0.975**	0.126	0.587	-0.285	0.663	-0.165	**0.881**	-0.143	**0.891**	0.010	-0.557	-0.306	**0.853**	0.012	0.606	-0.115
Sternal shield																		
SSL	**0.979**	0.069	**0.970**	0.199	0.310	**0.657**	0.675	0.591	**0.949**	-0.018	**0.918**	0.026	-0.494	-0.360	**0.879**	-0.126	**0.949**	0.048
SSW	**0.967**	0.094	**0.907**	-0.211	**0.820**	0.125	-0.071	**0.683**	**0.925**	-0.155	**0.711**	0.361	0.428	0.407	**0.884**	-0.406	0.421	**0.631**
S1–S1	**0.872**	0.376	**0.889**	0.266	0.080	**0.608**	-0.410	**0.617**	**0.855**	0.019	**0.862**	0.052	-0.419	**-0.743**	**-0.923**	0.291	**0.844**	0.174
S3–S3	**0.936**	0.295	**0.956**	0.184	0.261	0.415	**-0.767**	0.494	**0.934**	-0.225	0.563	0.031	-0.245	**-0.772**	**0.873**	0.414	**0.842**	0.023
S1L	**0.940**	-0.298	**0.929**	-0.228	**0.867**	0.162	**0.921**	0.085	**0.954**	0.192	**0.890**	-0.191	**-0.750**	0.028	-0.162	**0.654**	**0.881**	-0.089
S3L	**0.957**	-0.264	**0.978**	0.000	**0.765**	0.053	**0.940**	0.141	**0.969**	0.120	**0.972**	-0.016	**-0.923**	-0.022	**-0.717**	-0.487	**0.812**	-0.259

Table 1. *continued*

Body regions and characters	*Laelaps acuminata*								*Gigantolaelaps oudemansi*									
	All host taxa		*Euryoryzomys*		*E. nitidus* & *russatus*		*Oecomys*		All host taxa		*Euryoryzomys*		*E. nitidus* & *russatus*		*Oecomys*		*H. megacephalus*	
	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2
Epigynial shield																		
ESL	**0.913**	0.277	**0.984**	0.125	**0.748**	0.095	-0.098	**0.770**	**0.962**	0.024	**0.792**	0.209	-0.083	-0.501	-0.037	0.484	**0.926**	0.001
E5–E5	**0.932**	0.236	**0.921**	-0.154	**0.741**	-0.214	-0.526	**0.638**	**0.904**	0.057	**0.739**	0.094	-0.266	-0.447	0.111	**-0.901**	**0.868**	0.123
ESW	**0.934**	0.203	**0.965**	-0.134	**0.861**	0.151	-0.087	**0.871**	0.534	**0.731**	**0.854**	-0.307	**-0.771**	-0.017	0.031	**-0.670**	**0.931**	0.142
S4L	**0.938**	-0.264	**0.775**	-0.458	**0.868**	-0.228	**0.851**	0.166	**0.963**	0.173	**0.944**	0.135	-0.355	0.398	**-0.774**	-0.261	**0.878**	0.240
E5L	**0.945**	-0.262	**0.966**	0.015	0.698	0.011	**0.928**	0.208	**0.831**	0.424	**0.819**	-0.444	**-0.905**	0.259	0.551	**-0.650**	**0.713**	0.128
Anal shield																		
PARAL	**0.962**	0.118	**0.981**	0.084	**0.706**	0.103	0.418	0.197	0.697	**-0.649**	-0.193	-0.590	-0.432	**0.722**	-0.681	-0.454	0.671	-0.328
POSTL	**0.977**	0.048	**0.982**	0.113	**0.717**	-0.169	0.400	0.064	**0.799**	-0.511	0.397	-0.323	-0.417	**0.655**	**0.793**	-0.286	0.578	-0.302
POST–EDGE	**0.972**	0.076	**0.976**	-0.073	**0.836**	-0.007	0.119	-0.144	**0.816**	-0.119	0.283	0.579	0.453	0.003	-0.651	0.232	-0.336	-0.325
PARA–PARA	**0.974**	0.125	**0.965**	0.160	0.370	**0.625**	0.230	**0.740**	**0.853**	0.133	0.387	**0.688**	**0.705**	-0.139	0.660	-0.532	0.595	0.135
ASW	**0.968**	0.014	**0.859**	-0.373	**0.871**	0.076	0.344	**0.778**	**0.894**	-0.022	0.432	0.433	0.314	-0.085	0.127	**0.642**	**0.798**	0.020
Legs																		
PROXCOX	**0.885**	-0.155	0.695	**-0.616**	**0.878**	0.060	0.522	-0.397	**0.920**	-0.156	**0.874**	-0.255	**-0.804**	0.238	**0.970**	0.133	-0.444	-0.457
DISTCOX	**0.954**	-0.100	**0.885**	0.219	0.149	0.153	0.614	-0.027	**0.905**	-0.225	**0.772**	-0.371	**-0.749**	-0.283	**0.920**	-0.029	**0.826**	0.171
POSTCOX2	**0.977**	-0.104	**0.953**	-0.081	**0.722**	-0.269	**0.818**	-0.187	**0.843**	0.229	**0.921**	0.272	0.572	0.251	-0.533	0.505	**0.850**	-0.008
POSTCOX3	**0.916**	-0.086	0.557	-0.175	0.450	-0.165	0.362	-0.545	**0.887**	-0.320	0.269	**-0.782**	**-0.776**	0.050	**0.982**	-0.079	0.600	0.381
POSTCOX4	**0.965**	-0.065	**0.906**	0.228	-0.039	-0.205	0.566	-0.598	0.685	-0.378	**-0.742**	-0.377	-0.337	0.249	**0.818**	0.329	0.643	**0.603**
DFEM1L	**0.938**	0.104	**0.774**	-0.357	**0.739**	0.057	-0.143	**0.700**	**0.966**	0.085	**0.937**	0.162	-0.236	-0.183	0.670	0.020	**0.918**	-0.210
DGEN1L	**0.941**	-0.142	0.539	**-0.609**	**0.734**	-0.059	**0.739**	**0.603**	**0.904**	-0.180	**0.898**	0.317	0.266	-0.556	**-0.880**	-0.051	**0.737**	-0.437
Eigenvalue	**33.2**	**1.3**	**30.9**	**2.2**	**15.9**	**3.6**	**13.9**	**8.1**	**25.7**	**4.3**	**19.8**	**5.6**	**12.2**	**5.1**	**18.7**	**5.5**	**21.2**	**3.0**
% of variance	**89.7**	**3.5**	**83.5**	**5.9**	**43.0**	**9.7**	**37.6**	**21.9**	**69.5**	**11.6**	**53.5**	**15.1**	**33.0**	**13.8**	**50.5**	**14.9**	**57.3**	**8.1**

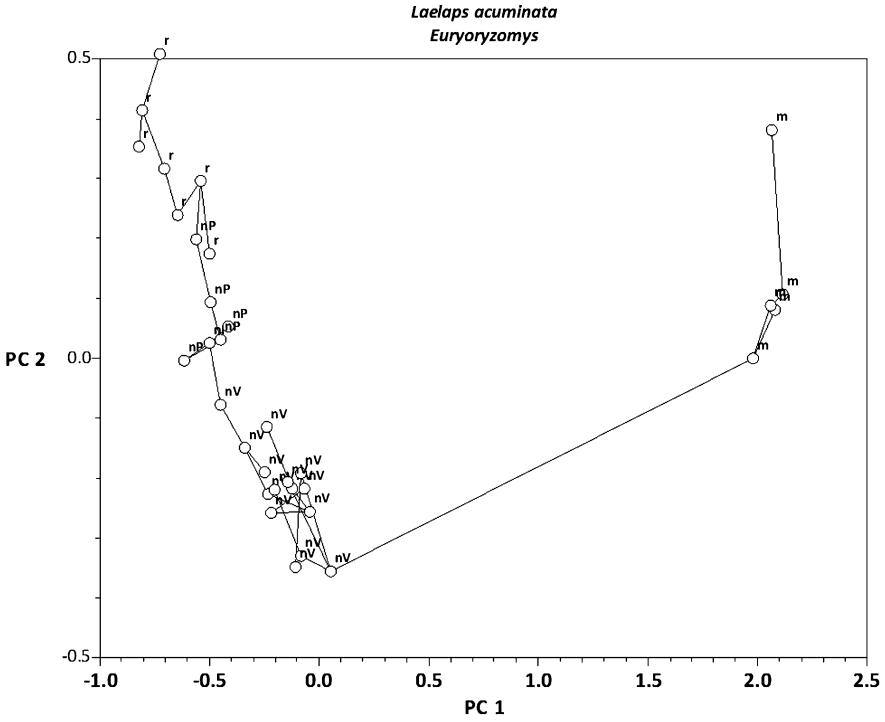

Figure 4. Matrix plot (PC 1 × PC 2) of *Laelaps acuminata* from *Euryoryzomys* spp. examined in this study. OTU codes indicate host species and country of origin: m, *Euryoryzomys macconnelli* (Brazil, Amazonas state); nP, *E. nitidus*, Paraguay (Depto. Itapúa); nV, *E. nitidus*, Bolivia (Depto. Santa Cruz); r, *E. russatus* (Brazil, São Paulo state). See Table 1 for character loadings on PC 1 and PC 2, and eigenvalues of these two components.

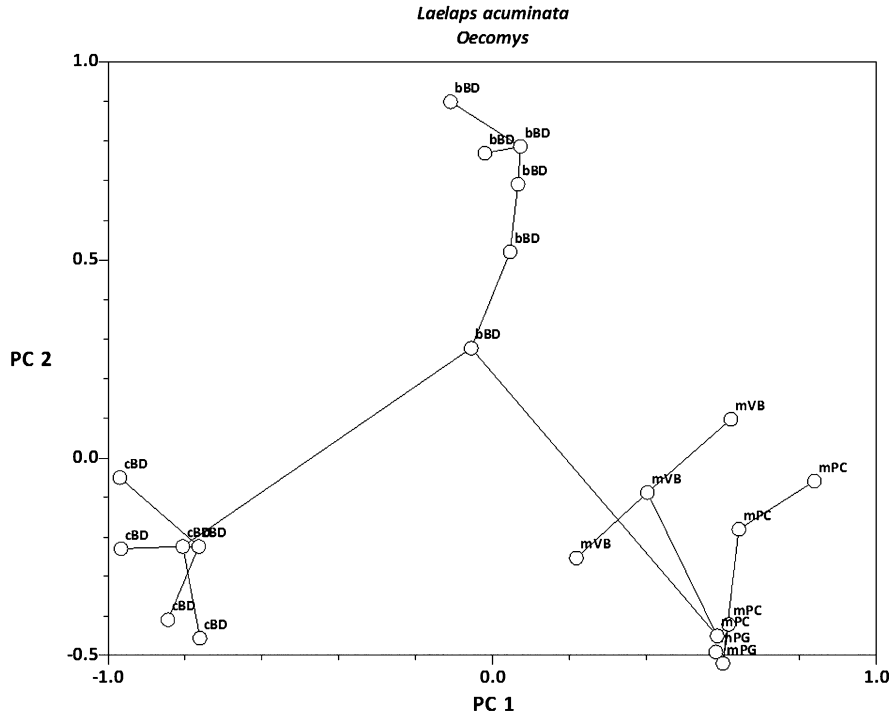

Figure 5. Matrix plot (PC 1 × PC 2) of *Laelaps acuminata* from *Oecomys* spp. examined in this study. OTU codes indicate host species, country, and department of origin: bBD, *Oecomys bicolor*, Brazil, Distrito Federal; cBD, *Oe. concolor*, Brazil, Distrito Federal; mPC, *Oe. mamorae*, Paraguay, Depto. Concepción; mPG, *Oe. mamorae*, Paraguay, Depto. Paraguarí; mVB, *Oe. mamorae*, Bolivia, Depto. Bení. See Table 1 for character loadings on PC 1 and PC 2, and eigenvalues of these two components.

***Oecomys* spp.**—Among the *L. acuminata* from *Oecomys* (Figure 5), PC-1 accounts for 37.6% of the variance, and has 13 characters strongly associated with it (12 positively, one negatively). The positively associated characters are distributed throughout most of the body regions (Table 1), and this is a general size component. This component separates the mites from *Oe. mamorae* (largest) from those of *Oe. concolor* (smallest) and *Oe. bicolor* (intermediate). PC-2 represents 21.9% of the variance, and has 11 characters associated strongly and positively with it (Table 1). These characters are from most of the body regions, but do not include characters from the dorsal chaetotaxy or gnathosoma. This component separates mites from *Oe. bicolor* (largest in those characters) from those from *Oe. concolor* and *Oe. mamorae* (both smaller in those characters).

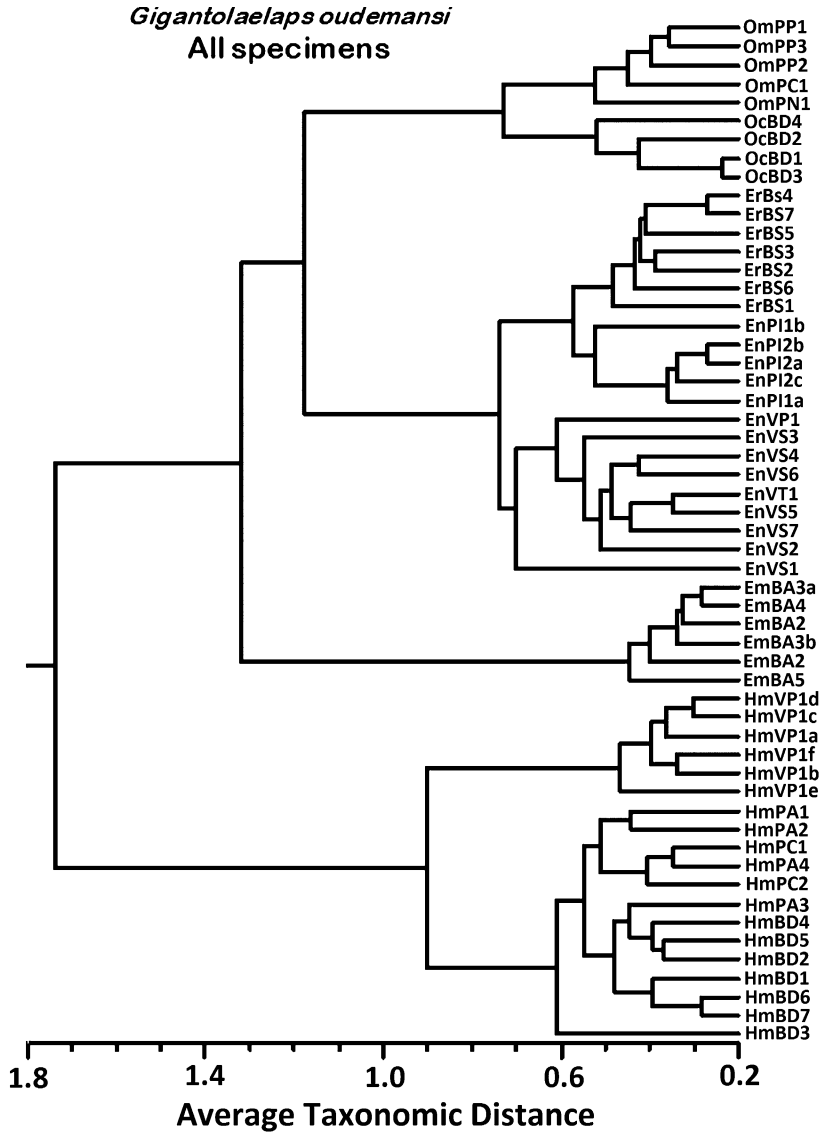

Figure 6. Phenogram depicting morphometric relationships among all *Gigantolaelaps oudemansi* used in this study. OTU codes refer to host species, locality, and individual: 1st and 2nd (letters), genus and species (Em, *Euryoryzomys macconnelli*; En, *E. nitidus*; Er, *E. russatus*; Hm, *Hylaeamys megacephalus*; Oc, *Oecomys concolor*; Om, *Oe. mamorae*); 3rd (letter), country (B, Brazil; P, Paraguay, V, Bolivia); 4th (letter), state (or department) (BA, Amazonas; BD, Distrito Federal; BS, São Paulo; PA, Amambay; PC, Concepción; PG, Paraguarí; PI, Itapúa; PN, Ñeembucú; PP, Alto Paraguay; VP, Pando; VS, Santa Cruz; VT, Tarija); 5th (number), host individual sequence number, of that species and state; 6th (letter, where present), mite individual sequence number of that species, state, and host individual. The cophenetic correlation coefficient is 0.837.

Gigantolaelaps oudemansi

All specimens.—The phenogram of all specimens of *G. oudemansi* together shows several distinct groups corresponding both to host species and to locality (Figure 6). All mites from *Hylaeamys* are clustered, and within this primary cluster, the Bolivian specimens are separate from the cluster of Brazilian and Paraguayan specimens. The mites from *Euryoryzomys macconnelli* also cluster together. Another cluster includes mites from *Oecomys*, with specimens from *Oe. concolor* and *Oe. mamorae* found in separate clusters. As with *Laelaps acuminata*, mites from *Euryoryzomys nitidus* and *E. russatus* are found together within one cluster, with the Bolivian *E. nitidus* mites clustering separately from the Paraguayan *E. nitidus* and Brazilian *E. russatus* mites, which also are found in separate terminal clusters.

A principal component analysis provides additional insight into the nature of the primary clusters found in the phenogram. PC1 accounts for 69.5% of the variance, and is a size component, with 30 of the 37 characters loading strongly and positively on this component. This component shows that *G. oudemansi* from *Euryoryzomys macconnelli* are approximately three standard deviations larger than those from *Hylaeamys megacephalus*, with mites from *E. nitidus*, *E. russatus*, and the *Oecomys* species intermediate in size (Figure 7). PC2 accounts for 11.6% of the variance, with three characters (two dorsal chaetotaxy, one epigynial shield) loading strongly and positively, and one (anal shield) loading negatively (Table 1). This axis clearly separates the *Oecomys* mites from all others, with the *Oecomys* mites being about one standard deviation larger on this component than the other specimens.

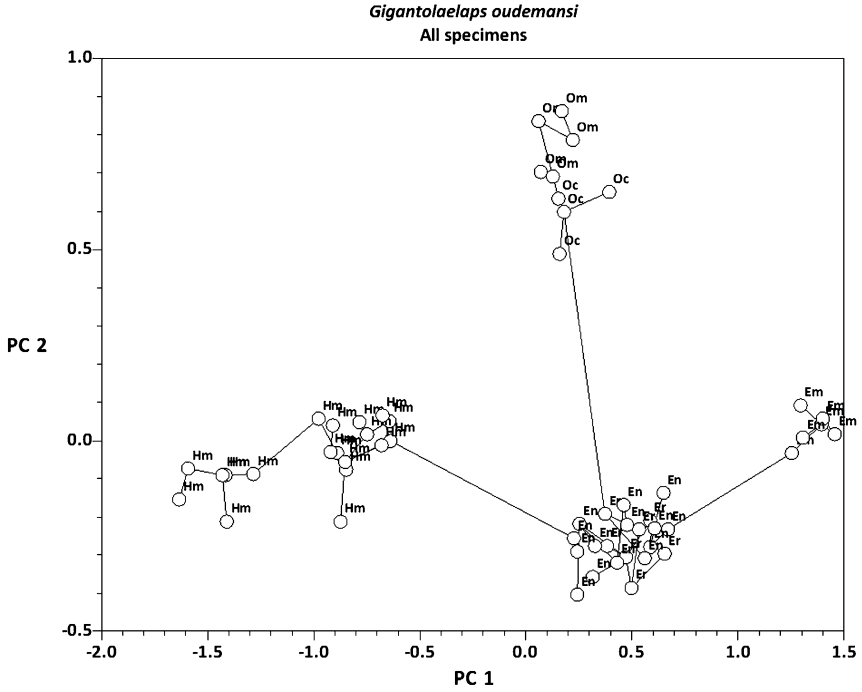

Figure 7. Matrix plot (PC 1 × PC 2) of all *Gigantolaelaps oudemansi* examined in this study. OTU codes indicate genus and species of host animal: Em, *Euryoryzomys macconnelli*; En, *E. nitidus*; Er, *E. russatus*; Hm, *Hylaeamys megacephalus*; Oc, *Oecomys concolor*; Om, *Oe. mamorae*. See Table 1 for character loadings on PC 1 and PC 2, and eigenvalues of these two components.

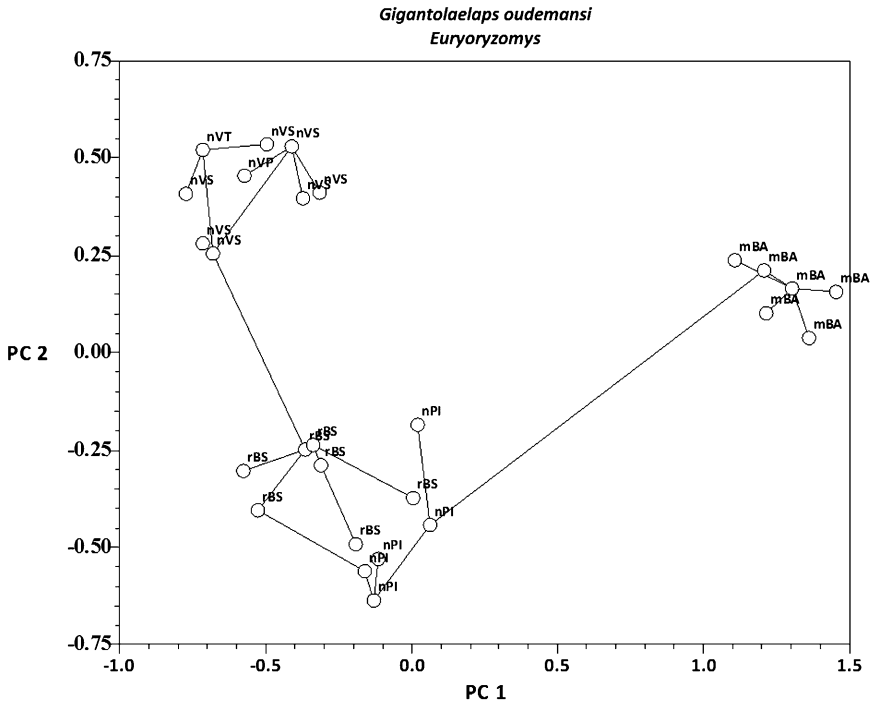

Figure 8. Matrix plot (PC 1 × PC 2) of *Gigantolaelaps oudemansi* from *Euryoryzomys* spp. examined in this study. OTU codes indicate host species, and country and department (state) of origin: mBA, *Euryoryzomys macconnelli*, Brazil (Amazonas); nPl, *E. nitidus*, Paraguay (Itapúa); nVP, *E. nitidus*, Bolivia, Depto. Pando; nVS, *E. nitidus*, Bolivia, Depto. Santa Cruz; nVT, *E. nitidus*, Bolivia, Depto. Tarija; rBS, *E. russatus*, Brazil (São Paulo). See Table 1 for character loadings on PC 1 and PC 2, and eigenvalues of these two components.

***Euryoryzomys* spp.**—Principal component 1 (PC-1) accounts for 53.5% of the variance, and serves to separate the *E. macconnelli* mites from those from *E. nitidus* and *E. russatus* (Figure 8). This is a general size component, with 22 characters (from all areas except anal shield) loading strongly and positively, and one character (from anal shield) loading strongly and negatively (Table 1). Thus (as with *L. acuminata*), mites from *E. macconnelli* are generally larger than those from the other two *Euryoryzomys* species. In contrast to PC-1, PC-2 accounts for 15.1% of the variance, and is a shape component, with one character (anal shield) loading positively, and two (dorsal chaetotaxy, legs) loading negatively. This component clearly separates individual clusters of the mites from Brazilian *E. russatus* and Paraguayan *E. nitidus*, from those from Bolivian *E. nitidus* (with those from *E. macconnelli* imtermediate on this axis).

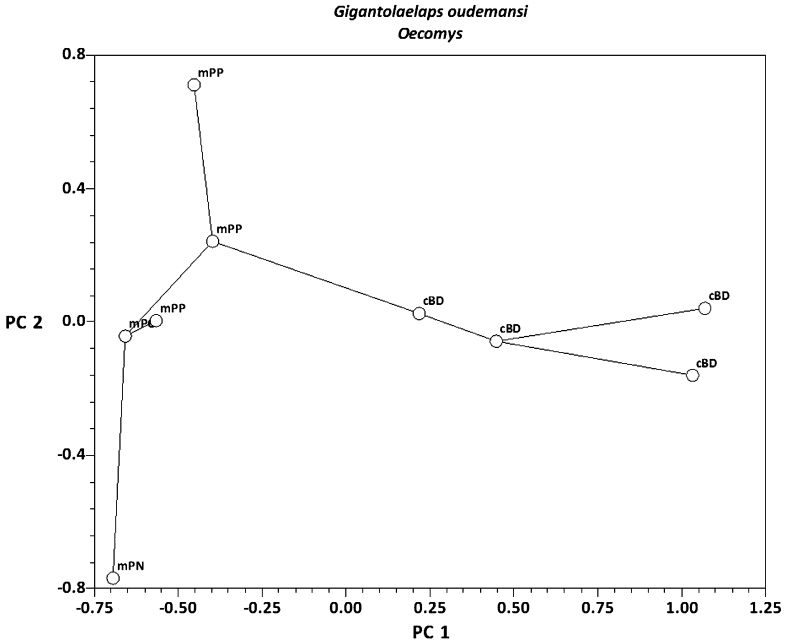

Figure 9. Matrix plot (PC 1 × PC 2) of *Gigantolaelaps oudemansi* from *Oecomys* spp. examined in this study. OTU codes indicate host species, and country and department (state) of origin: cBD, *Oe. concolor*, Brazil, Distrito Federal; mPC, *Oe. mamorae*, Paraguay, Depto. Concepción; mPN, *Oe. mamorae*, Paraguay, Depto. Ñeembucú; mPP, *Oe. mamorae*, Paraguay, Depto. Alto Paraguay. See Table 1 for character loadings on PC 1 and PC 2, and eigenvalues of these two components.

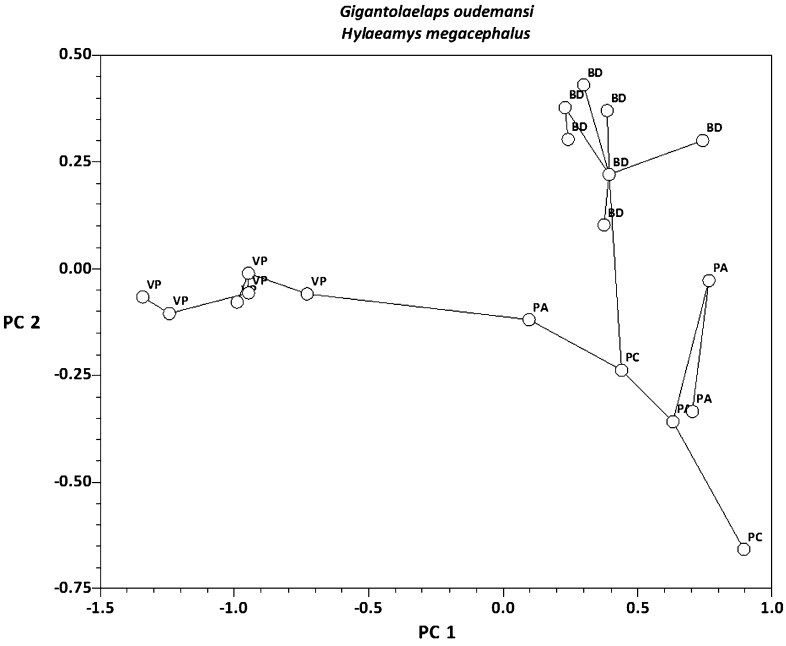

Figure 10. Matrix plot (PC 1 × PC 2) of *Gigantolaelaps oudemansi* from *Hylaeamys megacephalus* examined in this study. OTU codes indicate host animal's country and department of origin: Brazil (BD, Distrito Federal); Paraguay (PA, Amambay; PC, Concepción) or Bolivia (VP, Pando). See Table 1 for character loadings on PC 1 and PC 2, and eigenvalues of these two components.

***Oecomys* spp.**—The PCA of *G. oudemansi* from *Oe. concolor* and *Oe. mamorae* serves to separate mites from the two host species on PC-1, which accounts for 50.5% of the variance, and has 19 characters loading strongly (ten positively, nine negatively) (Table 1). Mites from *Oe. concolor* range from high to intermediate values, whereas those from *Oe. mamorae* have uniformly low values on this component (Figure 9). Although based on very few mite specimens, PC-2 (14.9%, two positive, four negative) may indicate a morphocline in these mites, with the single southern specimen (Ñeembucú) separated somewhat from the more northerly specimens (Concepción, Alto Paraguay).

***Hylaeamys megacephalus*.**—In the analysis of *G. oudemansi* infesting *H. megacephalus*, PC-1 is a size component, with 24 of the 37 characters loading strongly and positively, and accounting for 57.3% of the variance (Table 1). This axis separates the smaller Bolivian specimens from the larger specimens from Brazil and Paraguay (Figure 10). PC-2, although accounting for only 8.1% of the variance, and having only two characters strongly associated with it, serves to separate the Brazilian (Distrito Federal) from the Paraguayan (Amambay and Concepción) specimens, with the Brazilian specimens having consistently greater projection values on this axis.

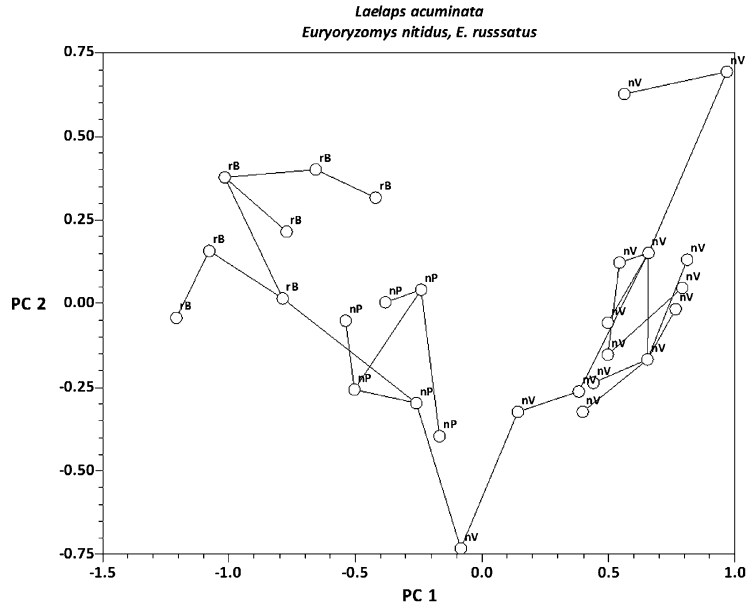

Figure 11. Matrix plot (PC 1 × PC 2) of *Laelaps acuminata* from *Euryoryzomys nitidus* and *E. russatus* examined in this study. OTU codes indicate host species and country of origin: nP, *E. nitidus*, Paraguay (Itapúa); nV, *E. nitidus*, Bolivia (Santa Cruz); rB, *E. russatus*, Brazil (São Paulo). See Table 1 for character loadings on PC 1 and PC 2, and eigenvalues of these two components.

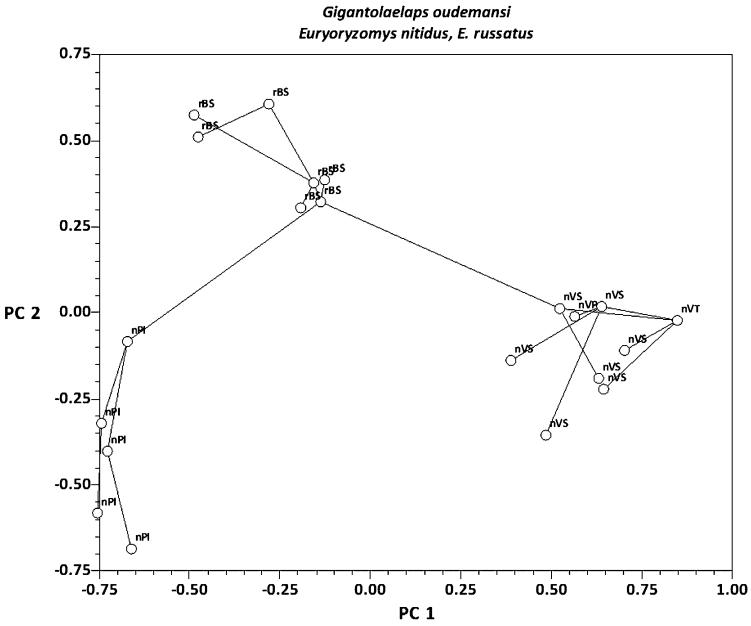

Figure 12. Matrix plot (PC 1 × PC 2) of *Gigantolaelaps oudemansi* from *Euryoryzomys nitidus* and *E. russatus* examined in this study. OTU codes indicate host species and country and department of origin: nPI, *E. nitidus*, Paraguay (Itapúa); nVP, *E. nitidus*, Bolivia (Pando); nVS, *E. nitidus*, Bolivia (Santa Cruz); nVT, *E. nitidus*, Bolivia (Tarija); rBS, *E. russatus*, Brazil (São Paulo). See Table 1 for character loadings on PC 1 and PC 2, and eigenvalues of these two components.

Laelapine mites from *Euryoryzomys nitidus* and *E. russatus*

Laelaps acuminata.—In the analysis of mites from only the two *Euryoryzomys* species (which clustered very closely in the PCA of all specimens from this host genus), 21 of 37 characters (from all body regions) load strongly and positively on PC-1, which accounts for 43% of the morphometric variance among these specimens (Table 1). Generally, the mites from *E. russatus* (Brazil) are smallest, those from Bolivian *E. nitidus* are largest, and those from Paraguayan *E. nitidus* are intermediate, although the three populations form a continuum along this axis (Figure 11). Six of 37 characters (from dorsal chaetotaxy, sternal shield, and anal shield) load strongly and positively on PC-2, which accounts for 9.7% of the variance. Mites from *E. russatus* tend to be larger on this axis than those from Paraguayan *E. nitidus*, whereas mites from Bolivian *E. nitidus* span the entire range of variation on PC-2.

Gigantolaelaps oudemansi.—One character (from the anal shield) loads strongly and positively on PC-1 (33.0% of the variance), and 12 characters (all other body regions) load strongly and negatively (Table 1). Thus (in contrast to *L. acuminata*), the mites from Bolivian *E. nitidus*, with higher projections on this axis, are generally smaller than the other *G. oudemansi* in this analysis. The specimens from *E. nitidus* from Paraguay are largest, with the mites from *E. russatus* being intermediate along PC-1 (Figure 12). Only two characters (sternal shield, legs) load strongly and pos-

itively on PC-2, which accounts for 8.1% of the variance. However, this axis differentiates the *E. russatus* mites from Paraguayan and Bolivian *E. nitidus*, which have lower projection values along PC-2. Nevertheless, the minimum spanning tree indicates that in terms of overall variation, mites from *E. russatus* lie in an intermediate position relative to those collected from Bolivian and Paraguayan populations of *E. nitidus* (Figure 12).

Discussion

Patterns of mite morphometric variation

In this study, several patterns were clearly and consistently observed in the morphometric variation of both nominal mite species: (1) mites from the same host individual cluster no more closely with each other, than with other mites of the same host species, from the same locality; (2) mites from the same host species cluster more closely with each other, than with mites from other host species; (3) among mites from a particular host species, individuals from the same locality tended to cluster more closely together, than to mites from other localities; and (4) mites from different host species from the same locality cluster no more closely together, than those from different host species from different localities. We discuss each of these patterns in order.

1. **Mites from the same host individual**.—The phenograms for both *L. acuminata* (Figure 2) and *G. oudemansi* (Figure 6) show several instances of from 2–6 mite specimens examined from the same host individual. Of 14 examples of this among *L. acuminata* (including mites from six host species, and from seven localities), two show the mites from the same host individual clustered most closely together, and in ten cases the cluster of mites from the same host includes at least one mite from another host (two cases were indeterminate, i.e., no other specimens from that host species, at that locality, were available). For *G. oudemansi* (three instances total), two were indeterminate, and the other clustered with mites from other host individuals. Thus, we observe that mites from the same host individual show no heightened tendency to cluster together, and conclude that the individual host itself is not a strong determinant of mite morphometric form, for either of these nominal laelapine species.

2. **Mites from the same host species**.—As observed for both *L. acuminata* and *G. oudemansi*, mites from the same host species cluster most closely together, with one exception which is seen for both mite species. Except for mites from *Euryoryzomys nitidus* and *E. russatus*, all mite specimens form clusters which reflect their host species. This is true across all host taxa, and regardless of specimens from multiple localities for any host species. This strongly suggests that the mites associated with each host species are genetically isolated from mites from other host species, i.e., are independent phylogenetic units (species), heretofore unrecognized, and awaiting formal description. This pattern also strongly supports the currently recognized species boundaries of the oryzomyine host species used in this study, with the apparent exception of *Euryoryzomys nitidus* and *E. russatus*.

3. **Geographic patterning within host-species clusters**.—Our data contain three instances of multiple localities represented within a mite host–species cluster, with each reflecting a geographic pattern. *Laelaps acuminata* from *Oecomys mamorae* includes specimens from three localities: Beni, Bolivia, and Concepción and Paraguarí, Paraguay. The two Paraguayan localities are relatively close to each other geographically, whereas Beni, Bolivia is several times more distant (Figure 1). Reflecting the disparity in inter-locality distances, the specimens from the two Paraguay locations cluster most closely together, and then cluster less closely with the Bolivian specimens (Figs. 2, 5). However, it is worth noting that the species boundaries of *Oecomys* are poorly understood (Carleton et al., 2009).

   Gigantolaelaps oudemansi also includes specimens from *Oe. mamorae* from multiple localities; however, these three localities (Alto Paraguay, Concepción, Ñeembucú) are all in Paraguay, and relatively near to each other (Figure 1). Although this is based on very few specimens, and thus inconclusive, these specimens appear to form a morphocline based on a few characters (PC 2, Figure 9), reflecting their south–north distribution.

   Specimens of *G. oudemansi* from *Hylaeamys megacephalus* were also examined from four widely-dispersed localities: Pando, Bolivia; Amambay and Concepción , Paraguay; and Distrito Federal, Brazil. As with the *L. acuminata* from *Oe. mamorae*, the specimens from northwestern Bolivia form a cluster separate from those from east of the Paraguay River in Paraguay (and Brazil, in this case). This pattern is seen in the phenogram (Figure 6) and the PCA plot (Figure 10), where the Bolivian specimens are widely separated along PC-1 (57.3% of the variation, a size component), from the "eastern" specimen group. In the same plot, the Brazilian specimens are distinguished from the Paraguayan ones along PC-2 (8.1% of the variation, loading strongly on only two characters).

Each of the three examples in our data exhibits what would be considered fairly standard and unsurprising geographic variation (reflecting both distance and ecoregional differences), if these host-based groups were recognized as distinct laelapine species. Although indirect, we suggest that this is additional evidence for the specific distinctness of these host-associated mite groups, independent of, and supportive of, the evidence provided by the consistent clustering of mites from the same host species.

4. **Mites from the same locality, but different host species, do not cluster together**.—Our data include four instances of mites of the same nominal species from the same locality, but from different oryzomyine host species: *L. acuminata* from Distrito Federal, Brazil (*Oecomys bicolor*, *Oe. concolor*); and *G. oudemansi* from Distrito Federal, Brazil (*Hylaeamys megacephalus*, *Oe. concolor*), Concepción, Paraguay (*H. megacephalus*, *Oe. mamorae*), and Pando, Bolivia (*Euryoryzomys nitidus*, *H. megacephalus*). In the three cases involving *G. oudemansi*, mites from the same localities are not closely clustered (Figs. 6, 7). *Laelaps acuminata* infesting *Oecomys bicolor* and *Oe. concolor* in Distrito Federal are more similar morphometrically, but the *Oe. bicolor* nevertheless cluster more closely with *Oe. mamorae* (from both Paraguay and Bolivia) than with *Oe. concolor* from Distrito Federal (Figure 2). Thus, it is clear that geographically-based clustering, or any geographic patterning, is found only within groups of mites infesting the same host species.

Species boundaries and distributions of oryzomyine hosts

Morphometric analysis has proven to be a valuable tool in revealing the presence of cryptic species within the nominal laelapine mites associated with South American sigmodontine rodents in Paraguay, both with akodontines (Gettinger & Owen, 2000) and rodents in palustrine habitats (Gettinger et al., 2011a). In these studies, the geographic scale was more limited and the analysis clearly showed that mite species boundaries were determined by the specificity of their associations with clearly defined host species. However, the present study embraces a much wider geographic scale, examining host–mite associations from widely separated localities and macrohabitats. As in previous studies, it is clear that *G. oudemansi* and *L. acuminata* are composite, with cryptic species infesting a range of closely related host species, when we compare patterns of mite morphometrics and the species boundaries and distributions of their oryzomyine hosts. Appendix 2 lists the type locality and author of the two nominal laelapine species and seven oryzomyine species considered in this study.

***Euryoryzomys* spp.**—Both nominal mite species associated with *E. macconnelli* are morphometrically distinct from those associated with *E. nitidus* and *E. russatus*, indicating that *E. macconnelli* may be more spatially or temporally isolated; in contrast, both mite species showed morphometric patterns that bring into question the current taxonomic understanding of species boundaries for *E. nitidus* and *E. russatus*. Although very few records are available, mice of the "*nitidus* group" have been reported from Paraguay and Argentina; Massoia (1974) reported specimens from Misiones province as "*Oryzomys capito intermedius*", and Myers (1982) also reported specimens from eastern Paraguay as "*O. intermedius*." Because *intermedius* (Leche, 1886) is a synonym of *Euryoryzomys russatus*, we can conclude that these mammalogists aligned these specimens with this species from the Atlantic Forest Region. However, when Musser et al. (1998) examined these specimens, they concluded that they were morphologically closer to specimens of *E. nitidus* from the Andean region. Our specimens from the "*nitidus* group" are from Itapúa department, in eastern Paraguay. Both *L. acuminata* (Figs. 2, 11) and *G. oudemansi* (Figs. 6, 12) from this host population clustered more consistently and closely with mites from *E. russatus*, than with mites infesting *E. nitidus* in Bolivia. Because the forests of Itapúa are considered extensions of the Atlantic Forests of southeastern Brazil, whereas Paraguayan and Bolivian populations of *E. nitidus* are separated by the Chacoan subregion, mite morphometric analysis supports the hypothesis that the Paraguayan *Euryoryzomys* are aligned with *E. russatus*. However, without a series of mite specimens from hosts collected between these widely separated localities, geographic variation cannot be ruled out, and it is not possible at present to assess whether these host and/or mite populations are isolated genetically.

***Oecomys* spp.**—The analyses of mites from *Oecomys* spp. show unequivocal separation of the three (for *L. acuminata*) or two (*G. oudemansi*) host species. Moreover, the two instances in which mites from a host species are available from more than one locality, both show geographic patterning which seems appropriately described as intraspecific morphometric variation. Thus, although *Oecomys* spp. are primarily arboreal (in contrast to the strongly terrestrial behavior of *Euryoryzomys* spp. and *Hylaeamys megacephalus*), the same pattern emerges for both nominal laelapine mites in fact comprising several heretofore unrecognized species, each of which appears to be associated with a single host species. Carleton et al. (2009) have shown that *Oe. concolor* and *Oe.*

mamorae, along with a new species, *Oe. sydandersoni* Carleton, Emmons, and Musser, 2009, share distinguishing morphological characteristics that distinguish them from other known species of *Oecomys*, including *Oe. bicolor*, the host studied here. It is noteworthy that although *G. oudemansi* infests both *Oe. concolor* and *Oe. mamorae*, it was not found in association with *Oe. bicolor* after intense sampling of this host in central Brazil (Gettinger, 1987). If these mites have cospeciated with their hosts, it is possible that the presence or absence of *G. oudemansi* may by phylogenetically informative.

Hylaeamys megacephalus.—Only one of our two measured mite species, *G. oudemansi*, was associated with *Hylaeamys megacephalus* (*L. acuminata* does not infest *Hylaeamys*). Specimens of *G. oudemansi* from central Brazil cluster together with specimens from Amambay and Concepción in Paraguay. *Hylaeamys megacephalus* is a component of the "gallery forest community" of the Cerrado Province in central Brazil (Mares et al., 1986) and these cerrado habitats and their gallery forests continue south into Paraguay, providing a habitat connection between the cerrados of central Brazil and eastern Paraguay. However, the morphometric analysis presented by Musser et al. (1998) raised some interesting questions, as the larger cranial and dental characteristics of the central Brazilian *H. megacephalus* (the same host specimens of our study mites) aligned these specimens with western Amazonian populations (which would include our Bolivian specimens). However, because chromosomal evidence did not support this connection, Musser et al. (1998) concluded that the small sample size available may have been misleading. Our morphometric analysis groups *G. oudemansi* from central Brazil and Paraguay, thus excluding the specimens from northern Bolivia, and supporting the chromosomal evidence followed by Musser et al. (1998). Biogeographically, this is the same pattern that both *L. acuminata* and *G. oudemansi* are suggesting for the *Euryoryzomys nitidus / E. russatus* populations.

Final comments

If mite morphometric patterns reflect gene flow within and among populations infesting different species of oryzomyine hosts, they support contemporary changes in the taxonomy of oryzomyine host groups (Musser et al., 1998; Weksler et al., 2006), and suggest that the mite taxonomy (e.g., Furman, 1972) is very conservative, substantially underestimating the diversity of laelapine species infesting oryzomyine rodents in the New World. The nominal species, *G. oudemansi* and *L. acuminata* infest many, but not all of the species formerly assigned to *Oryzomys* "*capito*" (Musser et al., 1998), as well as three other genera of oryzomyines (*Euryoryzomys*, *Hylaeamys*, and *Oecomys*), all closely grouped within "clade B" of Weksler (2006). Similar morphometric patterns are observed (Gettinger et al., 2011a) with another complex of laelapine mites infesting *Holochilus*, *Nectomys*, *Pseudoryzomys*, and *Sooretamys* in Paraguay ("clade D" of Weksler, 2006). Strong host specificity of laelapine mites for their particular host species reflects historical associations within the evolution of the Oryzomyini.

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Appendix 1. Mite specimens examined, host species, country, and state (Brazil) or department (Paraguay, Bolivia) of origin, deposit location and catalog number of host specimen (where known), and collector (or museum) field acronym and number. Museum acronyms are: AMNH, American Museum of Natural History; FMNH, Field Museum of Natural History; MNHNP, Museo Nacional de Historia Natural del Paraguay; MSB, Museum of Southwestern Biology (University of New Mexico); RDO, biological collections of Robert Owen, Asunción, Paraguay (under MOU with Secretaría del Ambiente, Paraguay, to hold specimens until the MNHNP is able to accept them); TTU, Natural Sciences Research Laboratory, Texas Tech University; UnB, Universidade de Brasilia; USNM, United States National Museum of Natural History. Asterisk following museum catalog number indicates host specimen which was examined and reported in Musser et al. (1998). Collector or museum acronyms are: AP, Alexandre Palma; BDP, Bruce Patterson; DG, Don Gettinger; FMNH, Field Museum of Natural History; KAE, Kristina Ernest; MAL, Jay Malcolm; NK, Museum of Southwestern Biology, University of New Mexico; TK, Natural Science Research Laboratory, Texas Tech University.

	Host		Locality				
Code	**Genus**	**Species**	**Country**	**Province**	**Museum & Catalog No.[1]**	**Collector Name**	**Collector Number**
Laelaps acuminata							
EmBA1	*Euryoryzomys*	*macconnelli*	Brazil	Amazonas	USNM580005*	MAL	2073
EmBA2	*Euryoryzomys*	*macconnelli*	Brazil	Amazonas		MAL	2095
EmBA3a	*Euryoryzomys*	*macconnelli*	Brazil	Amazonas	USNM580007*	MAL	2100
EmBA3b	*Euryoryzomys*	*macconnelli*	Brazil	Amazonas	USNM580007*	MAL	2100
EmBA3c	*Euryoryzomys*	*macconnelli*	Brazil	Amazonas	USNM580007*	MAL	2100
EnVS1	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	MSB55328*	NK	11819
EnVS2	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	AMNH260359*	NK	11823
EnVS3a	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	AMNH262026*	NK	12744
EnVS3b	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	AMNH262026*	NK	12744
EnVS4a	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	AMNH264182*	NK	22751
EnVS4b	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	AMNH264182*	NK	22751
EnVS5a	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	AMNH264184*	NK	22756
EnVS5b	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	AMNH264184*	NK	22756
EnVS6a	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	AMNH264185*	NK	22757
EnVS6b	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	AMNH264185*	NK	22757
EnVS7a	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	MSB67322*	NK	22801
EnVS7b	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	MSB67322*	NK	22801
EnVS7c	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	MSB67322*	NK	22801
EnVS7d	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	MSB67322*	NK	22801
EnVS8	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	MSB67321*	NK	22804
EnPI1a	*Euryoryzomys*	*nitidus*	Paraguay	Itapúa	TTU116547	TK	66255
EnPI1b	*Euryoryzomys*	*nitidus*	Paraguay	Itapúa	TTU116547	TK	66255
EnPI1c	*Euryoryzomys*	*nitidus*	Paraguay	Itapúa	TTU116547	TK	66255
EnPI1d	*Euryoryzomys*	*nitidus*	Paraguay	Itapúa	TTU116547	TK	66255
EnPI1e	*Euryoryzomys*	*nitidus*	Paraguay	Itapúa	TTU116547	TK	66255
EnPI1f	*Euryoryzomys*	*nitidus*	Paraguay	Itapúa	TTU116547	TK	66255
ErBS1	*Euryoryzomys*	*russatus*	Brazil	São Paulo	FMNH141638	BDP	2795
ErBS2	*Euryoryzomys*	*russatus*	Brazil	São Paulo	FMNH141641	BDP	2804
ErBS3	*Euryoryzomys*	*russatus*	Brazil	São Paulo	FMNH141737	BDP	2846
ErBS4	*Euryoryzomys*	*russatus*	Brazil	São Paulo	FMNH	BDP	2952
ErBS5	*Euryoryzomys*	*russatus*	Brazil	São Paulo	FMNH145422	BDP	3000
ErBS6	*Euryoryzomys*	*russatus*	Brazil	São Paulo	FMNH145427	BDP	3117
ErBS7	*Euryoryzomys*	*russatus*	Brazil	São Paulo	FMNH145428	BDP	3122
ObBD1a	*Oecomys*	*bicolor*	Brazil	DF	OMNH17482	DG	334
ObBD1b	*Oecomys*	*bicolor*	Brazil	DF	OMNH17482	DG	334
ObBD2	*Oecomys*	*bicolor*	Brazil	DF	OMNH17483	DG	479
ObBD3	*Oecomys*	*bicolor*	Brazil	DF	OMNH17480	KAE	80
ObBD4a	*Oecomys*	*bicolor*	Brazil	DF	UnB	AP	178

Appendix 1. *Continued.*

Code	Host		Locality		Museum & Catalog No.[1]	Collector Name	Collector Number
	Genus	Species	Country	Province			
ObBD4b	*Oecomys*	*bicolor*	Brazil	DF	UnB	AP	178
OcBD1a	*Oecomys*	*concolor*	Brazil	DF	UnB	AP	116
OcBD1b	*Oecomys*	*concolor*	Brazil	DF	UnB	AP	116
OcBD2a	*Oecomys*	*concolor*	Brazil	DF	UnB	DG	187
OcBD2b	*Oecomys*	*concolor*	Brazil	DF	UnB	DG	187
OcBD3	*Oecomys*	*concolor*	Brazil	DF	UnB	KAE	75
OcBD4	*Oecomys*	*concolor*	Brazil	DF	UnB	KAE	114
OmVB1a	*Oecomys*	*mamorae*	Bolivia	Bení	AMNH262012	NK	13158
OmVB1b	*Oecomys*	*mamorae*	Bolivia	Bení	AMNH262012	NK	13158
OmVB1c	*Oecomys*	*mamorae*	Bolivia	Bení	AMNH262012	NK	13158
OmPC1	*Oecomys*	*mamorae*	Paraguay	Concepción	RDO	TK	60610
OmPC2a	*Oecomys*	*mamorae*	Paraguay	Concepción	MNHNP	TK	61632
OmPC2b	*Oecomys*	*mamorae*	Paraguay	Concepción	MNHNP	TK	61632
OmPC2c	*Oecomys*	*mamorae*	Paraguay	Concepción	MNHNP	TK	61632
OmPG1a	*Oecomys*	*mamorae*	Paraguay	Paraguarí	RDO	TK	60545
OmPG1b	*Oecomys*	*mamorae*	Paraguay	Paraguarí	RDO	TK	60545
Gigantolaelaps oudemansi							
EmBA1	*Euryoryzomys*	*macconnelli*	Brazil	Amazonas		MAL	2061
EmBA2	*Euryoryzomys*	*macconnelli*	Brazil	Amazonas	USNM580005*	MAL	2073
EmBA3a	*Euryoryzomys*	*macconnelli*	Brazil	Amazonas		MAL	2095
EmBA3b	*Euryoryzomys*	*macconnelli*	Brazil	Amazonas		MAL	2095
EmBA4	*Euryoryzomys*	*macconnelli*	Brazil	Amazonas		MAL	2096
EmBA5	*Euryoryzomys*	*macconnelli*	Brazil	Amazonas	USNM580007*	MAL	2100
EnVP1	*Euryoryzomys*	*nitidus*	Bolivia	Pando	AMNH262960	NK	14158
EnVS1	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	MSB55328	NK	11819
EnVS2	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	AMNH260359	NK	11823
EnVS3	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	AMNH262026	NK	12744
EnVS4	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	MSB56073	NK	13001
EnVS5	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	MSB56062	NK	13078
EnVS6	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	AMNH264182	NK	22751
EnVS7	*Euryoryzomys*	*nitidus*	Bolivia	Santa Cruz	AMNH264184	NK	22756
EnVT1	*Euryoryzomys*	*nitidus*	Bolivia	Tarija	MSB67358	NK	23448
EnPI1a	*Euryoryzomys*	*nitidus*	Paraguay	Itapúa	TTU116547	TK	66255
EnPI1b	*Euryoryzomys*	*nitidus*	Paraguay	Itapúa	TTU116547	TK	66255
EnPI2a	*Euryoryzomys*	*nitidus*	Paraguay	Itapúa	RDO	TK	66256
EnPI2b	*Euryoryzomys*	*nitidus*	Paraguay	Itapúa	RDO	TK	66256
EnPI2c	*Euryoryzomys*	*nitidus*	Paraguay	Itapúa	RDO	TK	66256
ErBS1	*Euryoryzomys*	*russatus*	Brazil	São Paulo	FMNH141644	BDP	2816
ErBS2	*Euryoryzomys*	*russatus*	Brazil	São Paulo	FMNH141654	BDP	2852
ErBS3	*Euryoryzomys*	*russatus*	Brazil	São Paulo	FMNH145422	BDP	3000
ErBS4	*Euryoryzomys*	*russatus*	Brazil	São Paulo	FMNH145429	BDP	3131
ErBS5	*Euryoryzomys*	*russatus*	Brazil	São Paulo	FMNH145424	FMNH	145424
ErBS6	*Euryoryzomys*	*russatus*	Brazil	São Paulo	FMNH145427	FMNH	145427
ErBS7	*Euryoryzomys*	*russatus*	Brazil	São Paulo	FMNH145428	FMNH	145428
HmVP1a	*Hylaeamys*	*megacephalus*	Bolivia	Pando	AMNH262937*	NK	14157

Appendix 1. *Continued.*

Code	Host		Locality		Museum & Catalog No.[1]	Collector Name	Collector Number
	Genus	Species	Country	Province			
HmVP1b	*Hylaeamys*	*megacephalus*	Bolivia	Pando	AMNH262937*	NK	14157
HmVP1c	*Hylaeamys*	*megacephalus*	Bolivia	Pando	AMNH262937*	NK	14157
HmVP1d	*Hylaeamys*	*megacephalus*	Bolivia	Pando	AMNH262937*	NK	14157
HmVP1e	*Hylaeamys*	*megacephalus*	Bolivia	Pando	AMNH262937*	NK	14157
HmVP1f	*Hylaeamys*	*megacephalus*	Bolivia	Pando	AMNH262937*	NK	14157
HmBD1	*Hylaeamys*	*megacephalus*	Brazil	DF	OMNH17461	DG	098
HmBD2	*Hylaeamys*	*megacephalus*	Brazil	DF	UnB	DG	194
HmBD3	*Hylaeamys*	*megacephalus*	Brazil	DF	UnB	DG	299
HmBD4	*Hylaeamys*	*megacephalus*	Brazil	DF	UnB	DG	318
HmBD5	*Hylaeamys*	*megacephalus*	Brazil	DF	OMNH17466*	DG	393
HmBD6	*Hylaeamys*	*megacephalus*	Brazil	DF	OMNH17468*	DG	484
HmBD7	*Hylaeamys*	*megacephalus*	Brazil	DF	UnB	DG	494
HmPA1	*Hylaeamys*	*megacephalus*	Paraguay	Amambay	MNHNP	TK	61397
HmPA2	*Hylaeamys*	*megacephalus*	Paraguay	Amambay	MNHNP	TK	61425
HmPA3	*Hylaeamys*	*megacephalus*	Paraguay	Amambay	TTU116546	TK	61429
HmPA4	*Hylaeamys*	*megacephalus*	Paraguay	Amambay	RDO	TK	61437
HmPC1	*Hylaeamys*	*megacephalus*	Paraguay	Concepción	MNHNP	TK	60660
HmPC2	*Hylaeamys*	*megacephalus*	Paraguay	Concepción	MNHNP	TK	61512
OcBD1	*Oecomys*	*concolor*	Brazil	DF	OMNH17490	DG	503
OcBD2	*Oecomys*	*concolor*	Brazil	DF	OMNH17488	KAE	72
OcBD3	*Oecomys*	*concolor*	Brazil	DF	OMNH17487	KAE	76
OcBD4	*Oecomys*	*concolor*	Brazil	DF	UnB	KAE	114
OmPP1	*Oecomys*	*mamorae*	Paraguay	Alto Paraguay	MNHNP	TK	61050
OmPP2	*Oecomys*	*mamorae*	Paraguay	Alto Paraguay	RDO	TK	61108
OmPP3	*Oecomys*	*mamorae*	Paraguay	Alto Paraguay	RDO	TK	61110
OmPC1	*Oecomys*	*mamorae*	Paraguay	Concepción	RDO	TK	61457
OmPN1	*Oecomys*	*mamorae*	Paraguay	Ñeembucú	MNHNP	TK	66050

Appendix 2. Type localities for laelapine mite and oryzomyine rodent species mentioned in this article. UTM coordinates estimated by DG from map locality information as recorded by collector.

Laelaps acuminata Furman, 1972; ex. *Oecomys concolor*; Venezuela; Dto. Federal, 5 km N of Caracas [10°53′S, 66°95′W]

Gigantolaelaps oudemansi Fonseca, 1939; ex "field rats of undetermined species," Goias State, near Anapolis [16°33′S, 48°95′W]

Euryoryzomys macconnelli (Thomas, 1910); Guyana: Demerara Dist., Supenaam River, a tributary of the Lower Essequibo [06°79′N, 58°18′W]

Euryoryzomys nitidus (Thomas, 1884); Peru, Junin Dept., valley of Rio Tulumayo, 10 km S San Ramon, Amable Maria, 2000 ft. as located by Gardner & Patton, 1976 [11°12′S, 75°36′W]

Euryoryzomys russatus (Wagner, 1848); Brazil, Sao Paulo State, Ipanema [23°68′S, 46°71′W]

Hylaeamys megacephalus (Fischer, 1814); Paraguay, Canendiyu Dept., east of Rio Paraguay, 13.3 km (by road) N Curuguaty, 225m, as fixed by neotype designation by Musser et al, 1998 [24°47′S, 55°70′W]

Oecomys bicolor; Ecuador, Morona-Santiago Prov., Gualaquiza, Rio Gualaquiza, 885m [3°40′S, 78°57′W]

Oecomys concolor (Wagner, 1845); Brazil, Amazonas, Rio Curicuriari, a tributary of the Rio Negro, below Sao Gabriel [0°03′S, 67°09′W]

Oecomys mamorae (Thomas, 1906); Bolivia, Cochabamba Dept., upper Rio Mamoré, Mosetenes [16°66′S, 66°05′W]